METABOLIC RATE AND EVAPORATIVE WATER LOSS OF MEXICAN SPOTTED AND GREAT HORNED OWLS

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ABSTRACT.—We measured rates of oxygen consumption and evaporative water loss (EWL) of Mexican Spotted (*Strix occidentalis lucida*) and Great Horned (*Bubo virginianus*) owls in Arizona. Basal metabolic rate averaged 0.84 $ccO_2 \cdot g^{-1} \cdot h^{-1}$ for the Spotted Owl and 0.59 $ccO_2 \cdot g^{-1} \cdot h^{-1}$ for the Great Horned Owl, with apparent thermoneutral zones extending from 17.0–25.2°C for the Spotted Owl and 20.3–32.2°C for the Great Horned Owl. EWL increased exponentially with ambient temperature in both species, but the Great Horned Owl showed a greater ability to dissipate metabolic heat production at high temperatures than did the Spotted Owl. Body temperature of Spotted Owls was significantly higher above than below the upper critical temperature (25.2°C), whereas body temperature of Great Horned Owls did not differ significantly with ambient temperature. Gular flutter was first observed in Spotted Owls at 30°C and in Great Horned Owls at 37°C. The lower ability of the Spotted Owl to dissipate heat via evaporative cooling may partially explain its tendency to use habitats featuring cool microsites. *Received 18 Feb. 1993, accepted 1 June 1993.*

The Spotted Owl (*Strix occidentalis*) is most common in multilayered, closed-canopy forests throughout much of its range (Gould 1977, Forsman et al. 1984, Ganey and Balda 1989). Because of reductions in the amount of such habitat, the Spotted Owl is considered to be in jeopardy in many areas (Dawson et al. 1987, Thomas et al. 1990, Turner 1993). Understanding why Spotted Owls occupy these forests could provide insight into how to preserve or manage habitat for Spotted Owls. Barrows (1981) suggested that Spotted Owls are relatively intolerant of high temperatures and occupy multilayered forests to avoid high daytime temperatures (see also Gould 1977, Barrows and Barrows 1978, Forsman et al. 1984). Behavioral observations support this hypothesis. At ambient temperatures ≥27°C, Spotted Owls expose their legs and the pads of their feet, erect their contour feathers, droop their wings, and fan their rectrices away from the body (Barrows and Barrows 1978, Barrows 1981). Gular flutter is initiated at ambient temperatures as low as 29°C (Barrows and Barrows 1978), lower than reported for other owls inhabiting temperate environments (Ligon 1969).

In this study, we compared the metabolic rate and evaporative water

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loss of Mexican Spotted (*S. o. lucida*) and Great Horned (*Bubo virginianus*) owls from Arizona at different ambient temperatures. Mexican Spotted Owls typically occupy cool habitats featuring closed-canopy coniferous and deciduous forests, shaded cliffs, and/or caves (Ganey et al. 1988, Ganey and Balda 1989). Summer daytime temperatures observed in their roost areas typically are <25°C (Ganey et al. 1988), although nearby ambient temperatures may be considerably higher. In contrast, Great Horned Owls are found from the Sonoran Desert to high-elevation mixed-conifer forests in Arizona (Phillips et al. 1964) and are thus exposed to higher temperatures than are Spotted Owls. If thermoregulatory ability is important in habitat selection by Mexican Spotted Owls, such ability should differ significantly between Spotted Owls and species that range more widely.

METHODS

Three Great Horned and four Spotted Owls were used in metabolic tests. Great Horned Owls were obtained in late March from a rehabilitation center in Phoenix, Arizona, and housed in Flagstaff (elevation 2135 m) until metabolic rate determinations began. Spotted Owls were captured within 80 km of Flagstaff at elevations ranging from 2070–2370 m. Great Horned Owls were tested from late May through late June and Spotted Owls from July through mid-September. All Spotted Owls were released at the point of capture following completion of metabolic rate determinations.

Owls were housed in individual metal cages (1 m × 1 m × 2 m) supplied with a tree branch for use as a perch. Cages were located in a secluded outdoor courtyard, and were surrounded by trees and shrubs so that owls could perch in either sun or shade. Owls were fed a diet of white laboratory mice and rats, and fresh water was always available in the cage.

Rates of oxygen consumption ($\dot{V}O_2$) and evaporative water loss (EWL) were measured simultaneously during daylight hours, when owls are generally least active (Wijnandts 1984). Owls were placed in a 13-L metabolic chamber (20 cm in diameter by 41 cm high) equipped with a wooden perch. The chamber, constructed of PVC pipe with plexiglass top and bottom and fitted with airtight connections for plastic tubing, was placed inside a darkened, temperature-controlled incubator (accuracy ±0.2°C). Dry air was drawn through the chamber and an Applied Electrochemistry S-3A oxygen analyzer. Dry air was obtained by drawing room air through a plastic tube filled with Drierite. $\dot{V}O_2$ rates were calculated from the percent of oxygen removed from the air by the owl and the flow rate (2000 ml·min⁻¹ in all tests) corrected to standard temperature and pressure.

Food was removed from an owl's cage 24 h before tests began, and all owls were assumed to be postabsorptive. Owls were weighed to the nearest gram immediately before tests began to allow calculation of mass-specific metabolic rates. Metabolic measurements were recorded at two or three temperatures per day. Owls were placed in the chamber between 08:00 and 09:00 h MST and allowed to come to rest (1–1.5 h) before measurements began. $\dot{V}O_2$ was then calculated every 5 min during a temperature trial of ≥1 h. A 1-h pause between trials allowed the owl to equilibrate to a new temperature. The order in which owls were exposed to temperatures was reversed between owls, to eliminate the potential influence of time in the chamber or temperature sequence on $\dot{V}O_2$. All temperature changes between subsequent trials were ≤5°C.

Because owls were sometimes active in the chamber during metabolic trials, we used the

lowest steady-state value of $\dot{V}O_2$ to estimate basal metabolism. We assumed that an owl had reached a steady state when $\dot{V}O_2$ remained constant during four or five complete turnovers of air within the chamber, approximately 20–25 mins.

Traditional models relating $\dot{V}O_2$ to ambient temperature (T_a) contain three segments. Below a lower critical temperature (LCT), $\dot{V}O_2$ decreases linearly with increasing T_a. Within the thermoneutral zone between the LCT and an upper critical temperature (UCT), $\dot{V}O_2$ is constant. Above the UCT, $\dot{V}O_2$ increases with increasing T_a. We used piecewise linear regression (Neter et al. 1989, pp. 370–373) to estimate the relationship between T_a and $\dot{V}O_2$ and to estimate LCT and UCT. This technique is useful where the relationship between the dependent and independent variables varies in different ranges of the independent variable (Neter et al. 1989). It allows quantitative definition of "join points" where the relationship between variables changes (i.e., LCT and UCT) and is thus ideally suited for use with metabolic data.

We attempted to fit both two-segment models and traditional three-segment models. The equation used for a two-segment model was:

$$\dot{V}O_2 = \begin{cases} a_1 + b_1T, & T < c \\ a_2 + b_2T, & T \geq c, \end{cases}$$

where $a_2 = a_1 + c(b_1 - b_2)$ to ensure continuity at the join point, c. The equation used for a three-segment model was:

$$\dot{V}O_2 = \begin{cases} a_1 + b_1T, & T < c_1 \\ a_2, & c_1 \leq T < c_2 \\ a_3 + b_3T, & c_2 \leq T, \end{cases}$$

where $a_2 = a_1 + c_1b_1$ and $a_3 = a_2 - c_2b_3$ to ensure continuity at the join points, c_1 (=LCT) and c_2 (=UCT). We compared model fit using the extra sum of squares approach (Neter et al. 1989, Section 8.1) and retained the simplest model unless a more complex model explained significantly more of the variation in $\dot{V}O_2$.

EWL was determined by inserting a plastic tube filled with Drierite into the flow line leaving the metabolic chamber. This tube was weighed to the nearest 0.1 mg before and after a metabolic test, with the change in weight representing EWL by the animal. We used exponential regression models (Neter et al. 1989, Section 15.2) to estimate the relationship between T_a and EWL. Because effectiveness of evaporative cooling varies with relative humidity (RH), we estimated the RH in the chamber at different temperatures using equation 3 from Lasiewski et al (1966).

Body temperature (T_b) was measured using a flexible thermistor probe inserted into the cloaca and a YSI multichannel telethermometer (accuracy ±0.5°C). To minimize stress to the owl, body temperatures were recorded only at the conclusion of a day's testing, and were therefore not available for all owls at all T_a.

We estimated dry thermal conductance (C_{dry}; $J \cdot g^{-1} \cdot h^{-1} \cdot °C^{-1}$) using the formula:

$$C_{dry} = (20.1\dot{V}O_2 - 2.45EWL/T_b - T_a)$$

where $20.1\dot{V}O_2$ = metabolic heat production and $2.45EWL$ = evaporative heat loss, assuming that 1 mg H_2O = 2.45 J and 1 ccO_2 = 20.1 J (Withers and Williams 1990). We scaled C_{dry} to surface area following methods in Drent and Stonehouse (1971).

RESULTS

Mass-specific $\dot{V}O_2$ was lower at all temperatures in the Great Horned Owl than in the Spotted Owl (Fig. 1). A three-segment regression model explained significantly more of the variation in $\dot{V}O_2$ than a two-segment
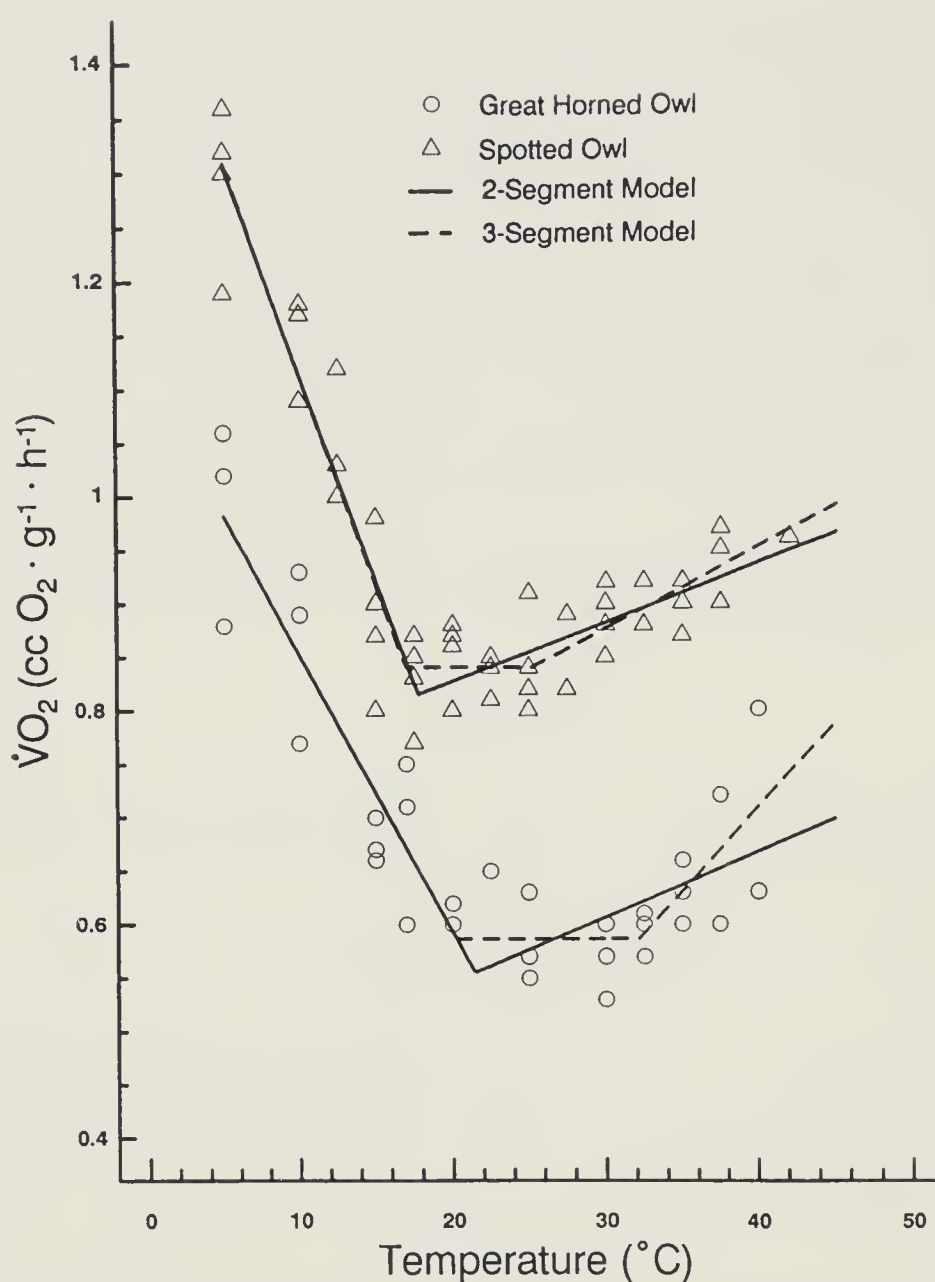
FIG. 1.   Oxygen consumption (observations and regression lines) of Mexican Spotted and Great Horned owls in Arizona at different ambient temperatures. Regression lines are shown for both two- and three-segment models.

model for the Great Horned Owl (comparison between models: $F = 4.44$, $P = 0.045$), but not for the Spotted Owl ($F = 1.65$, df $= 1, 42$, $P = 0.207$ for the best of the three-segment models attempted; Table 1).

Basal metabolic rate (BMR) averaged 0.59 $ccO_2 \cdot g^{-1} \cdot h^{-1}$ for the Great Horned Owl, with the thermoneutral zone extending from 20.3–32.2°C (Fig. 1). A thermoneutral zone could be defined for the Spotted Owl, but this model did not explain more of the variation in $\dot{V}O_2$ than a two-segment model (Fig. 1, Table 1). The best fit obtained using a three-segment model resulted in estimates of LCT at 17.0°C and UCT at 25.2°C. BMR of Spotted Owls averaged 0.84 $ccO_2 \cdot g^{-1} \cdot h^{-1}$ within this range of temperatures.

Rates of EWL increased exponentially with T_a in both species (Fig. 2).

TABLE 1

PARAMETER ESTIMATES (AND STANDARD ERRORS, WHERE AVAILABLE) FOR BEST-FITTING PIECEWISE REGRESSION MODELS RELATING $\dot{V}O_2$ TO T_a FOR GREAT HORNED AND MEXICAN SPOTTED OWLS

Param- eter[a]	Great Horned Owl		Mexican Spotted Owl	
	Two-segment model	Three-segment model	Two-segment model	Three-segment model
A1	1.112 (0.043)	1.112 (0.040)	1.499 (0.031)	1.505 (0.035)
B1	−0.026 (0.003)	−0.026 (0.003)	−0.039 (0.002)	−0.039 (0.003)
C1	21.5 (1.4)	20.3 (1.3)	17.7 (0.6)	17.0 (0.7)
A2	0.425	0.586	0.717	0.840
B2	0.006 (0.003)		0.006 (0.001)	
C2		32.2 (2.4)		25.2 (3.5)
A3	0.082			0.649
B3		0.016 (0.007)		0.008 (0.003)
R²	0.820	0.845	0.904	0.907
SE	0.060	0.057	0.046	0.046

[a] Parameters: A1, A2, and A3 = y intercepts for the first, second, and third segments of the regression model, respectively. B1, B2, and B3 = slopes for the three segments. By definition, B2 = 0 for 3-segment models. C1 and C2 = lower and upper critical temperatures, respectively. SE (standard error of the estimate) = square root of the residual sum of squares. General form of the regression equations is: $VO_2 = Ax + Bx(T_a)$, where x = segment number.

Regression equations describing the relationship between EWL and T_a were: Great Horned Owl, EWL = 0.36 exp($0.065T_a$), R^2 = 0.88, SE = 0.49 (standard error = square root of residual mean squares); Spotted Owl, EWL = 1.08 exp($0.043T_a$), R^2 = 0.89, SE = 0.46. These models differed significantly between species (F = 60.0, df = 2, 75, P < 0.001). Mass-specific EWL was higher in the Spotted than in the Great Horned owl. Maximum values measured (mg $H_2O \cdot g^{-1} \cdot h^{-1}$) were 5.5 for Great Horned Owls at 40°C and 6.2 for Spotted Owls at 42°C.

The ratio of heat dissipated by evaporative cooling to heat produced metabolically (EWL/HP) also increased exponentially with T_a (Fig. 3). Regression equations relating this ratio to T_a were: Great Horned Owl, EWL/HP = 0.075 exp($0.062T_a$), R^2 = 0.92, SE = 0.076; Spotted Owl, EWL/HP = 0.145 exp($0.043T_a$), R^2 = 0.90, SE = 0.064. Again, the models differed significantly between species (F = 10.2, df = 2, 75, P < 0.001). The ratio increased more rapidly in the Great Horned than in the Spotted owl. At the upper range of test temperatures, Great Horned Owls were able to dissipate nearly 100% of their metabolic heat, whereas Spotted Owls dissipated only 75–80% of their metabolic heat through respiratory evaporation. RH at $T_a \geq$ 30°C was higher during tests involving Great Horned Owls ($\bar{x}$ = 71.9 ± 7.1%, N = 7) than during tests involving Spotted Owls ($\bar{x}$ = 59.4 ± 2.7%, N = 10). Thus, Great Horned Owls were able
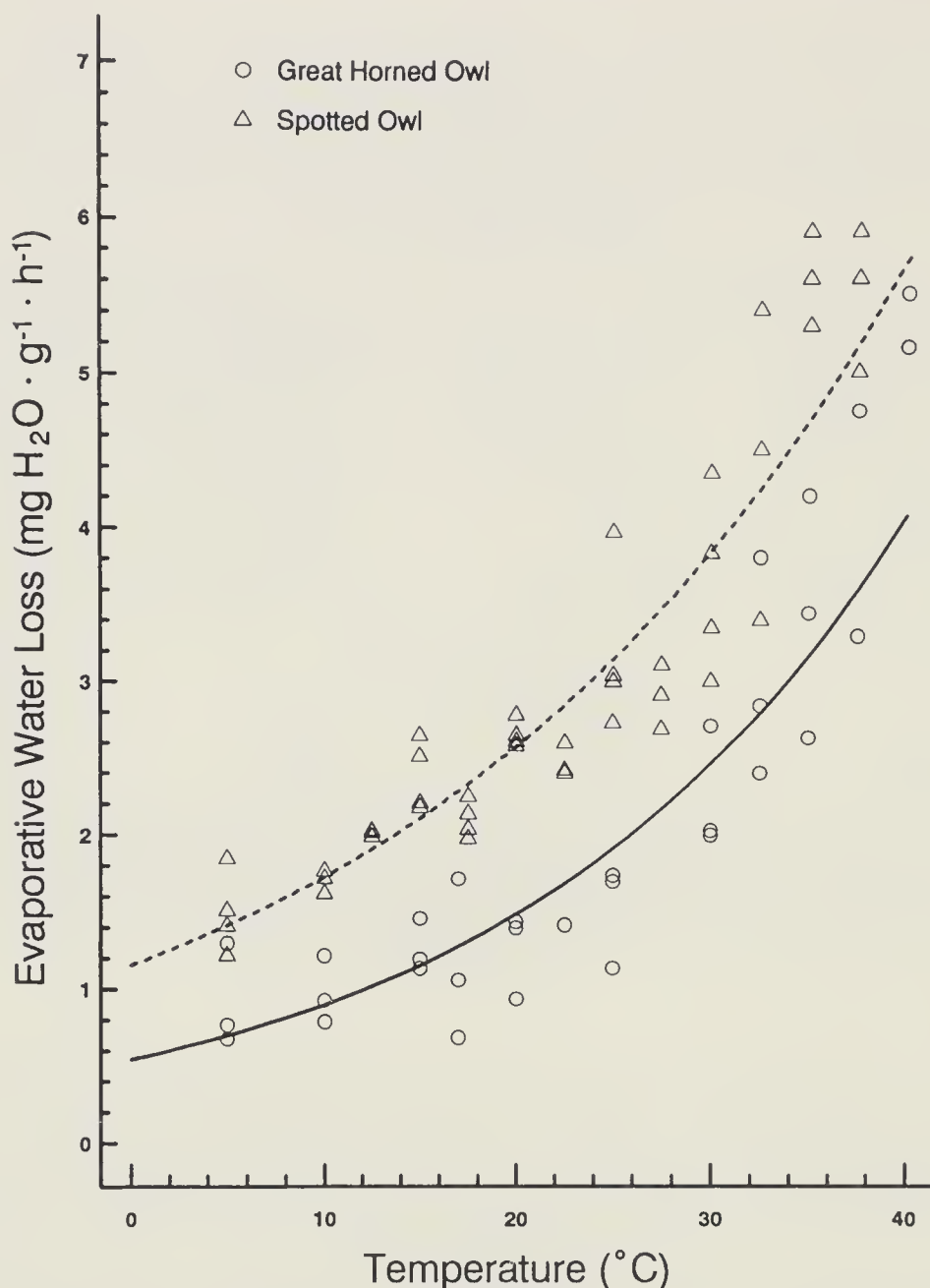
FIG. 2. Evaporative water loss (observations and exponential regression) of Mexican Spotted and Great Horned owls in Arizona at different ambient temperatures.

to dissipate a higher percentage of metabolic heat through evaporative cooling than Spotted Owls despite being exposed to conditions less favorable for evaporative cooling.

T_b of Great Horned Owls averaged 39.9°C (SE = 0.2, range = 39.0–41.0°C, N = 16), and did not vary predictably with T_a. T_b of Spotted Owls ranged from 38.5–42°C ($\bar{x}$ = 39.8 ± 0.2°C, N = 22), and was significantly higher above than below the UCT ($\bar{x}$ = 40.7 ± 0.2°C, N = 10, vs 39.1 ± 0.1°C, N = 12; Mann-Whitney U = 2.5, P = 0.0001). Estimates of T_b obtained from extrapolating the first segment of the regression equation to the x axis were: Spotted Owl, 38.4 and 38.6°C, two-and three-segment models, respectively; Great Horned Owl, 43.1°C (both models).

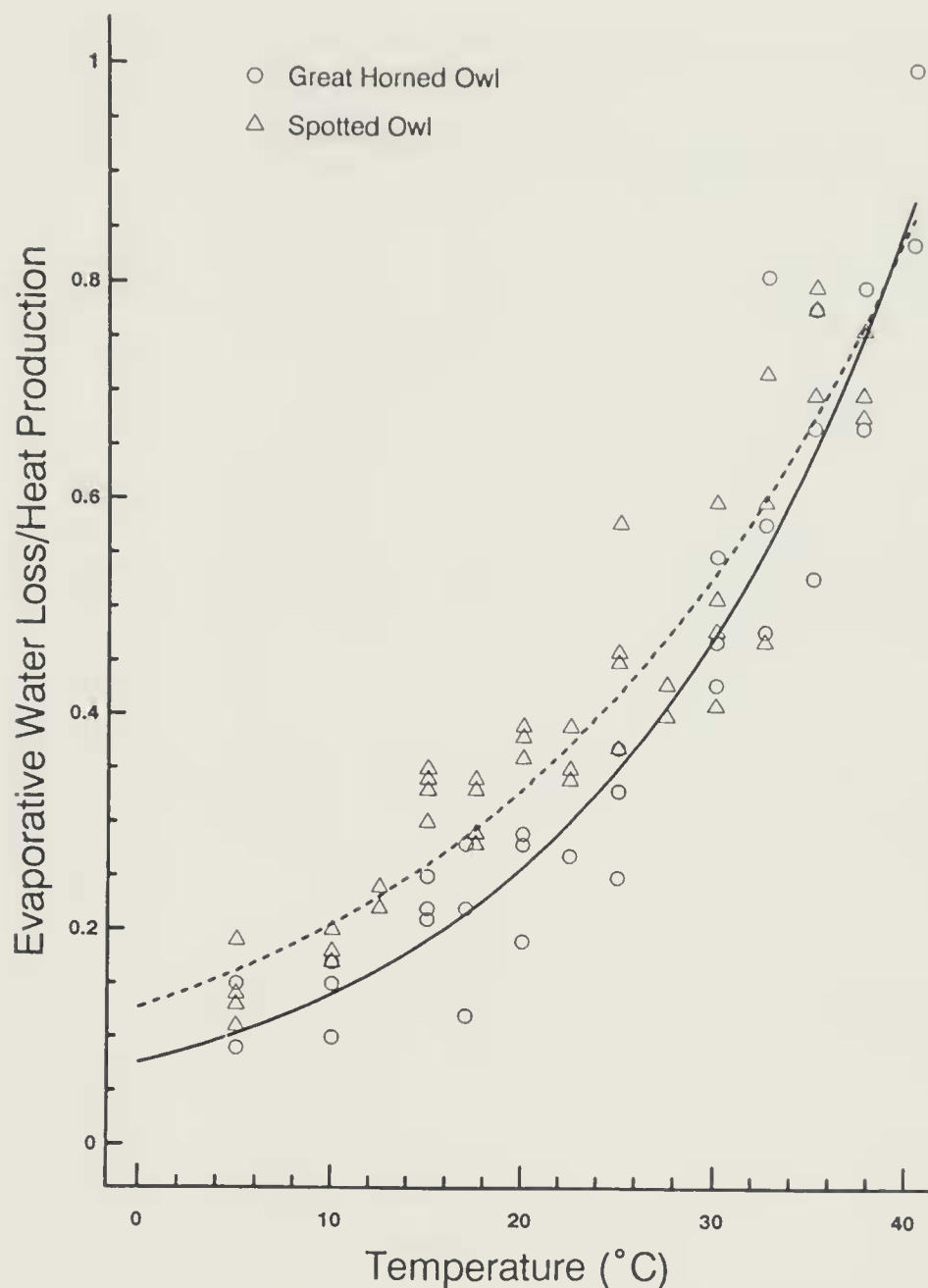Mass-specific C_{dry} was essentially constant in both species below the

FIG. 3.   Ratio of heat dissipated through evaporative cooling to metabolic heat production (observations and exponential regression) in Mexican Spotted and Great Horned owls at different ambient temperatures.

UCT and increased above the UCT. Average values for C_{dry} ($J \cdot g^{-1} \cdot h^{-1} \cdot$ °C^{-1}) below the UCT were: 0.49 ± 0.01 for Great Horned Owls and 0.59 ± 0.01 for Spotted Owls. Values for C_{dry} scaled to surface area (kj[m$^2 \cdot$h · °C]$^{-1}$) were 4.9 for Great Horned Owls and 4.8 for Spotted Owls.

We were able to note owl behavior only by opening the incubator door and observing the owl through the clear top of the metabolic chamber at the end of a trial. At temperatures ≥30°C, Spotted Owls drooped their wings as much as possible within the chamber, perched upright to expose the legs and feet, and erected their contour feathers. Intermittent gular flutter was observed in one Spotted Owl at 30°C, and rapid gular flutter was observed in all Spotted Owls by 32.5°C. Gular flutter was not observed

TABLE 2

AGREEMENT BETWEEN OBSERVED AND PREDICTED VALUES FOR VARIOUS PHYSIOLOGICAL CHARACTERISTICS OF GREAT HORNED AND MEXICAN SPOTTED OWLS IN ARIZONA[a]

Variable	Great Horned Owl			Spotted Owl		
	Observed	Predicted	Predicted (%)	Observed	Predicted	Predicted (%)
BMR						
(owls)	279.9	271.5	103	231.4	177.5	130
(NPs)	279.9	350.6	80	231.4	232.3	100
C_{dry}	0.49	0.47	104	0.59	0.63	94

[a] Predicted values obtained using equations based on average body mass. Sources: Basal Metabolic Rate (BMR; kj·day^{-1}) equation for owls from Wijnandts (1984), equation for nonpasserines (NPs) from Kendeigh et al. (1977); Dry Thermal Conductance (C_{dry}; J·g^{-1}·h^{-1}·°C^{-1}) from Herreid and Kessel (1967). Average body mass = 571 g for Spotted Owls and 1000 g for Great Horned Owls.

in Great Horned Owls until 37.0°C, and became constant only at higher temperatures. Great Horned Owls also perched upright and erected the contour feathers at temperatures >35°C but did not droop their wings.

DISCUSSION

Metabolic parameters may vary with taxonomic affinity (Kendeigh et al. 1977). Owls have lower mass-specific metabolic rates than nonpasserine birds, which have lower rates than passerines (Kendeigh et al. 1977, Wijnandts 1984). Mass-specific BMR of Great Horned Owls in this study fell between values predicted for owls and other nonpasserines (Table 2), was comparable to BMR reported for Great Horned Owls in Missouri (290.4 kj·day^{-1}, Kasparie 1983), and was intermediate between values reported by Pakpahan et al. (1989) for male (335.5 kj·day^{-1}) and female (262.7 kj·day^{-1}) Great Horned Owls in Michigan. Mass-specific BMR of Spotted Owls was 30% higher than predicted values for owls and roughly equal to values predicted for nonpasserines (Table 2). Mass-independent metabolism (ccO$_2$·h^{-1} [g$^{0.67}$]$^{-1}$; Bucher 1986) was 5.9 for the Great Horned Owl and 6.8 for the Spotted Owl.

There are several possible reasons for the observed differences in metabolism between these species. Restlessness during metabolic trials could cause inflated estimates of BMR. Unless Spotted Owls were consistently more restless than Great Horned Owls, however, restlessness does not explain the higher BMR observed in the Spotted Owl. After data screening (see Methods), variability in $\dot{V}O_2$ among birds at a given temperature did not appear to differ greatly between species (Fig. 1), and variability within trials was virtually identical for both species (average standard deviation of measurements of $\dot{V}O_2$ within a trial: Spotted Owl = 0.59, Great Horned

Owl = 0.61). Thus, we have no evidence that the observed difference between species was caused by differences in activity levels.

Another potential explanation for the observed BMR relates to the timing of this study. Weathers and Caccamise (1978) noted that BMR of birds >200 g is higher in summer than in winter. Coulombe (1970) reported that BMR of the Burrowing Owl (*Speotyto cunicularia*) was 29% higher during summer than during winter, although Wijnandts (1984) did not find significant seasonal differences in BMR of Long-eared Owls (*Asio otus*). Only two of the 16 data sets from the literature used by Wijnandts (1984) to develop the predictive equation for owls represented studies conducted during the summer (seven winter studies and seven unknown; Wijnandts [1984], Table 17), and both Kasparie (1983) and Pakpahan (1989) measured BMR during the winter or spring period. Thus, little of the data available for comparison was collected during the summer months, and predicted values may not accurately reflect summer BMR.

All Spotted Owls tested were molting heavily during the testing period. We conducted most metabolic trials with Spotted Owls during July and August, when Forsman (1981) reported peak rates of molt. BMR of Long-eared Owls increased 18% during periods of heavy molt (Wijnandts 1984). Assuming that BMR of Spotted Owls observed here was 18% higher than normal brings BMR closer to predicted values. Great Horned Owls were also molting during the testing period, however. If BMR of Great Horned Owls is also higher during molt, then BMR of these owls may fall well below predicted values at other times.

Despite these complicating factors, the data presented here should allow valid comparisons between species, because both species were tested using the same equipment and methodology and during the same season.

Mass-specific EWL was higher for the Spotted Owl than for the Great Horned Owl at all temperatures. At low temperatures, the ratio of EWL to metabolic heat production (Fig. 3) was also higher in the Spotted Owl than in the Great Horned Owl. By 40°C this trend was reversed, suggesting that the Great Horned Owl has a greater capacity to dissipate metabolic heat via evaporative cooling than does the Spotted Owl.

The slight but significant elevation of T_b in Spotted Owls at $T_a \geq 25°C$ suggests that EWL may not have been sufficient to dissipate metabolic heat at these temperatures. Thus, the upper range of test temperatures may have approached the upper limits at which the Spotted Owl is able to maintain constant T_b. Because the death of a Spotted Owl during testing was considered politically unacceptable, we did not attempt to determine the upper limit of temperature tolerance for this owl.

Mass-specific C_{dry} was higher in the Spotted Owl than in the Great

Horned Owl (Table 2). C_{dry} was 4% higher than predicted in the Great Horned Owl, however, and 6% less than predicted in the Spotted Owl. C_{dry} was virtually identical between species when computed on the basis of surface area, suggesting that passive heat transfer is roughly equivalent in these owls.

This study did not measure several factors that may affect thermoregulation in Spotted Owls in the wild. Barrows (1981) reported that owls reduced gular flutter during or following windy periods, presumably because of convective cooling (Hayes and Gessaman 1980). Because owls in the metabolic chamber were not exposed to cooling winds, they were unable to dissipate heat in this fashion.

The size of the metabolic chamber also limited the owl's ability to droop the wings away from the body and fan the rectrices, activities commonly observed in wild birds during hot weather (Barrows and Barrows 1978, Barrows 1981). This constraint would also limit the owl's ability to dissipate heat, particularly in conjunction with lack of exposure to cooling wind gusts. Thus, several potential avenues of passive heat loss were denied the owls during this study.

At least one important avenue of heat gain was also omitted from the study. Barrows (1981) noted that owls in sunlight showed more signs of distress on hot days than owls in shade, presumably because of solar radiation (Hayes and Gessaman 1980). Thus, the data presented here do not address the full range of factors influencing thermoregulation in Spotted Owls.

In general, this study supports field observations suggesting that Spotted Owls become uncomfortable at ambient temperatures >27°C (Barrows and Barrows 1978, Barrows 1981). It also supports the hypothesis that thermoregulation is better developed in the Great Horned than in the Spotted owl. The higher metabolic rate of Spotted Owls results in greater heat production. Reduced powers of evaporative cooling make it more difficult for the Spotted Owl to dissipate this metabolic heat. These physiological differences may partially explain the differences in habitat selection between these owls, particularly the tendency for Spotted Owls to use habitats featuring cool microsites.

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